THE DISTRIBUTION AND ABUNDANCE OF UNGULATES IN THE NORTHERN YELLOWSTONE ECOSYSTEM IN PRISTINE TIMES AND TODAY

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THE DISTRIBUTTON AND ABUNDANCE OF UNGULATES IN THE NORTHERN YELLOWSTONE ECOSYSTEM IN PRISTINE TIMES AND TODAY.[a]

By

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To describe how the northern Yellowstone ecosystem today differs from what it was in pristine times obviously requires that we know what it is like today, that we define when pristime times occurred, and that we know what the ecosystem was like back then. I believe we can reasonably describe the situation today, and we can somewhat arbitrarily define when pristine times occurred. But, like others (Chase 1986:115; Despain et al. 1986:7), I do not believe that we know now, nor are we likely to ever have a clear or useful idea of what the ecosystem was like in pristine times. This specifically applies to determining differences in the distribution and abundance of ungulates then and now.

I will define pristine times as prior to when European man had a direct or indirect influence on the ecosystem. This would be at least prior to the early 1800's. I believe that pristine times must be viewed as a period of time rather than a point in time. The period should be long enough to include the range of expected short-term variations that would have occurred in the ecosystem, but not long enough to include longer term trends in climate, soils, or species characteristics. A fundamental question is whether or not the kind of variation in ungulate distribution and abundance that has characterized modern times also occurred during pristine times. The answer to this question is crucial to evaluating the extent that ungulates, vegetation, and soils coevolved in pristine times and whether or not modern conditions should be viewed as a continuation of that process or as a significant departure from it.

The northern Yellowstone, or the northern Yellowstone ecosystem or winter range as I prefer to label it, is loosely defined as the area within and adjacent to Yellowstone National Park where elk (Cervus elaphus), mule deer (Odocoileus hemionus), pronghorn (Antilocapra americana), bighorn sheep (Ovis canadensis), bison (Bison bison athabascae), and moose (Alces alces); which range over

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much of the Park during summer, spend the late fall through spring period. A seventh species, the white-tailed deer (Odocoileus virginianus), may still range in low numbers along the Yellowstone River at the northern extremes of the ecosystem, but has not consistently ranged within the Park since the 1920's.

The northern Yellowstone ecosystem encompasses roughly 104,000 ha (257,000 acres) of which about 83,000 ha (205,000 acres) or 80% is within the Park and 21,000 ha (52,000 acres) are in the Yellowstone River valley and adjacent mountain slopes north of the Park, at least as far north as Six Mile Creek (Swenson, unpublished).

Disagreement among scientists and land managers, and thus public confusion, has prevailed for many years over how closely the condition of the northern Yellowstone today resembles its condition in pristine times. There are basically 2 schools of thought. One school believes that ungulates, particularly elk, were either absent or much less abundant in the ecosystem, especially during winter, in pristine times than now and that they did not become a prominent component and ecological force in the ecosystem until the direct and indirect influences of European man forced ungulates, specifically elk, from other areas into less suitable but less exploited habitats in and near the Park. According to this school of thought the elk population subsequently irrupted in the late 1890's and early 1900's, crashed during the winter of 1919-1920, and has since remained at levels that were uncharacteristic of the ecosystem in pristine times, with resulting effects on other components of the ecosystem that also did not occur in pristine times (Chase 1986). The other school of thought believes that ungulates, specifically elk, have been prominent components of the ecosystem from the time that suitable habitat developed following deglaciation of the Yellowstone region about 12,000 years ago. This school also believes that ungulates, particularly elk, were not forced into the Yellowstone region, that ungulates, including substantial numbers of elk, have always wintered in the ecosystem and in the Park, that there was no irruption and subsequent crash of the elk population, and that current conditions, while not the same as in pristine times, do not depart enough from those conditions to warrant correction by manipulative management, at least inside the Park (Houston 1982, Despain et al. 1986).

So which interpretation is correct? Is either one correct? Or can we ever know? In addressing my topic, I drew on recent synopses of the differing schools of thought about the ecosystem (Chase 1986, Houston 1982, Despain et al. 1986), my own research and experience in Yellowstone National Park from 1962 to 1970 (Barmore 1980), and on extensive review of scientific literature relevant to the norther Yellowstone issue through 1986 (exclusive of archeological or anthropological literature). I will concentrate on ungulate distribution and abundance during winter when these species, especially elk, have used the northern Yellowstone the most in modern times. I will also give special attention to elk because,

as we shall see shortly, this species has been ecologically dominant during modern times.

As of the mid-1980's, at least 16,000 elk, 400-500 bison, 1,800-2,000 mule deer, 180-200 bighorn sheep, 300-400 pronghorn, and perhaps 200 moose ranged within the ecosystem during the fall through spring period (Despain et al. 1986, Yellowstone National Park 1983). Most individuals of all these species except the pronghorn range far beyond the northern Yellowstone winter range during summer. The total biomass of ungulates consisted of about 90% elk, 5% bison, 3% mule deer, 1% moose, 0.4% pronghorn, and 0.3% bighorn sheep (biomass estimates for individuals of each species are from Houston 1982:157, Table 10.1).

The distribution of the ungulates within the winter range varies throughout the fall through spring period in relation to the availability of food, which is largely determined by the amount produced during summer, the depth and condition of the snow cover, and the cumulative amount of forage utilized by the ungulates. As the winter progresses, the ungulates generally concentrate on smaller portions of the winter range and move more extensively to lower elevations down the Yellowstone River inside and outside the Park. This general distributional pattern occurs all winters, but can vary considerably between years depending on the severity of snow conditions. These factors plus the nature of hunting seasons and other activities outside the Park affect the relative numbers of ungulates that range inside and outside the Park. A significant change in the distribution of elk since the population increased from a low of 4,000-5,000 in the mid-1960's has been the rather consistent migration of large numbers of elk to the lowest elevation, northernmost part of the ecosystem regardless of winter conditions (Swenson, unpublished).

The various ungulate species differ greatly in the amount of the winter range they use during fall through spring. Depending on snow conditions; elk, bison, and moose can range over most of the 104,000 ha (257,000 acres) during at least part of this period. Mule deer occupy about 15,000 ha (37,000 acres) of which about 35% is within the Park. Bighorn sheep occupy about 5,000 ha (12,000 acres) of which 88% is in the Park. Pronghorn occupy about 2,900 ha (7,000 acres) of which 75% is within the Park (Houston 1982:158, 160).

The pronghorn population that ranges in the Park is at the upper margin of its winter range relative to snow depth and requires habitats outside the Park to survive particularly severe winters. Most mule deer also migrate out of the Park during severe winters. Since the mid-1960's some bighorn sheep that summer in the Park have recolonized winter range in the Cinnabar Mountain area outside the Park (Keating 1982). In recent years a major part of the wintering bison population also has rather consistently migrated to lower elevations just within and outside the Park boundary

(Despain et al. 1986:38-45). This contrasts sharply with the situation since at least the late 1800's (Meagher 1973:85 and Appendix VI). Artificial feeding and other management practices probably kept the bison herd in the interior of the Park through 1952. Cessation of the feeding operation then, maintenance of the herd at a low level (80-200) through the mid-1960's, and the long traditional association with interior portions of the winter range probably kept the bison from ranging to lower elevations until the population developed new migration patterns that may be more characteristic of their behavior before bison were nearly exterminated in the Park region during the late 1800's.

The historical record from at least the 1920's to the present, which is more complete and reliable than for earlier years, indicates that all 6 ungulates species have coexisted within the ecosystem. During this period differences in the relative proportions of the several species and in their distribution and abundance were largely due to management activities inside and outside the Park that varied in kind and intensity (Barmore 1980, Houston 1982). Activities included hunting outside the Park and control by livetrapping and shooting inside the Park that reduced wintering populations to 4,000-5,000 elk, 150 pronghorn, and 80 bison in the 1960's. At these low population levels, few elk and essentially no bison dispersed out of the Park, but the entire pronghorn population still left the Park during the severe winter of 1967-68.

Prior to the 1920's to the earliest historical records in the 1830's, our knowledge about the distribution and abundance of the ungulates gets progressively fuzzier, which provides increasingly fertile ground for speculation and alternative interpretations of conditions. A major point of contention is whether or not the elk population irrupted during the late 1890's and early 1900's to an unprecedented high of over 30,000 and then crashed during the winter of 1919-1920 with calculated mortality of more than 10,000 elk (Chase 1986:14-21; Houston 1982:10-15, Appendices II and III; Despain et al. 1986:30-31). The records indicate that these events occurred on paper but not in the field. The best guess about the distribution and abundance of ungulates from the late 1880's into the 1920's is that substantial numbers of elk and smaller numbers of the other ungulate species wintered in the northern Yellowstone ecosystem inside and outside the Park. Bison numbers remained extremely low through 1900 due to poaching. The actual numbers of the various species or their relative distribution within the ecosystem and the Park cannot be accurately estimated.

Extensive market hunting and poaching from perhaps the 1870's into the 1880's probably reduced the numbers and altered the distribution of some or all of the 7 ungulate species from what they were prior to that time. But, again, the extent that numbers were reduced or how hunting and poaching influenced the distribution of the ungulates is unknown. Following tighter and better enforced

hunting regulations outside the Park and cessation of hunting and poaching inside the Park in the late 1880's, ungulate populations, particularly elk but not bison, increased to higher levels in the early 1900's that may have been more representative of conditions in the early 1800's.

The historical record from the early 1800's on does not support the idea (Chase 1986) that ungulates, particularly elk, were rare or absent from the northern Yellowstone area, especially during winter, until ungulates were forced into this area from other regions that were more heavily exploited by European man. A more probable scenario is that resident ungulate populations outside the Yellowstone region were nearly exterminated while the less exploited populations in the Yellowstone region persisted and became more apparent to increasing numbers of explorers and travelers (Houston 1982:24, Despain et al. 1986:29, Thomas and Toweill 1982:23, 35). The Park as a whole and the northern Yellowstone winter range specifically were not biological vacuums for any of the ungulate species as far back as historical records go; i.e., the 1830's, with or without a full complement of large mammalian predators or the influences of native Americans or European man. From our general knowledge about ungulate-habitat relationships, particularly the great ecological adaptability of elk, we can infer that this presence of ungulates in the northern Yellowstone region would have prevailed from the time that suitable habitats and tolerable winter conditions developed following deglaciation of the Yellowstone region about 12,000 years ago. But just how long ago is uncertain.

Moose were not reported on the winter range until about 1913, although they were present in other parts of the Park by the early second half of the 19th century (Houston 1982). One guess as to why moose were absent from the northern Yellowstone is that they were slower to colonize the Yellowstone region following deglaciation than the other ungulates. However, even though moose were not reported on the winter range specifically until 1913, they were reported on the Buffalo Plateau on the northern fringe of the winter range in 1870 (Henderson 1870 as cited in Houston 1982:205). Perhaps prospectors, miners from the Cooke City area, and market hunters in the 1860's-1880's eliminated the vulnerable and accessible moose from the travel route through the northern Yellowstone, and moose did not recover and reoccupy the area until regulations against hunting in the Park were effectively enforced.

So, finally, we have speculated our way backwards in time and closer to pristine times. Now more attention needs to be given to two factors that may have been more important ecological forces then than in modern times: (1) native Americans as fire brands and predators of ungulates and (2) other large mammalian predators, particularly the gray wolf (Canis lupus).

One school of thought suggests that elk were rare or absent in the prestine ecosystem and that mule deer, bighorn sheep, and pronghorn were relatively more numerous. This idea is largely based on the lack of elk remains at archeological sites in the Yellowstone region (Chase 1986:79,88,102-103). But why would elk but not the other ungulate species be absent from the ecosystem, particularly since the elk is very adaptable ecologically (Thomas and Toweill 1982:18,20). The proffered explanation is that for millenia, extensive, efficient, and selective predation by native Americans greatly reduced ungulate populations in the Yellowstone region from what they otherwise would have been (Chase 1986:97-105). On this point about all I can do is ask some questions that come to an ecologist's mind and hope that Dr. Frison will elaborate on the role of native Americans as predators of ungulates in the Yellowstone region during his presentation this afternoon.

If predation by native Americans was extensive enough to keep elk numbers low for millenia, why haven't their remains shown up in archeological sites? Did elk truly abandon the Yellowstone region for lower elevations where native Americans could have then preyed on them sufficiently to control their numbers? But wouldn't such heavy predation at low elevations have tended to force the elk back into the more remote Yellowstone region, as some individuals have proposed that European man did in the 1800's? What time of year would native Americans have been effective predators? Could they have been effective during summer when the ungulates would have been more widely dispersed at higher elevations and when plant food would have been more abundant and available to the native Americans? Studies on the evolution of steppe vegetation west of the Rocky Mountains, which is similar to that on the northern Yellowstone winter range, suggest that this vegetation may have evolved without heavy utilization by ungulates, such as elk and bison, at least during the summer growing season (Mack and Thompson 1984). This could mean that most ungulates, particularly elk and bison, were either scarce in the Yellowstone region year round, or that they were present in the region even in large numbers and merely abandoned the low elevation, steppe vegetation during summer, as they do now and have done historically, to disperse widely over much larger areas at higher elevations where the quantity or quality of food would have been more favorable for the ungulates, but where hunting by native Americans would have been more difficult and unprofitable and perhaps unnecessary due to the availability of plant foods. Would native Americans have preyed on the ungulates most effectively during winter when they were most concentrated? If so, would they have hunted them in the eastern portion of the winter range, where winter conditions would have been harsh for man and beast, or at lower elevations, where winters would have been less harsh? Would native Americans have extensively burned vegetation in the higher parts of the winter range to deplete the forage that elk and bison would need during winter, thus forcing them to lower elevations where living conditions during winter would have been better for the native Americans and hunting would have been easier?

A recent synthesis of what is known about elk ecology and management deals extensively with the relationships between elk and native Americans and suggests that predation by them was not great enough to exterminate elk or keep them at low numbers. The author concludes that, considering estimated numbers of elk and native Americans prior to the early 1800's, the distribution of native Americans, their primitive technology and limited mobility, and the seasonal habits of elk, "Indians likely had little adverse effects on elk populations. To the contrary, they may have been conducive to producing and maintaining healthy elk herds...." (McCabe 1982:65, 82-83,90).

There is increasing evidence, however, that native Americans, through their deliberate and accidental use of fire, were a significant ecological force in some areas during pristine times (Gruell 1985, 1986; McCabe and McCabe 1984; McCabe 1982; Chase 1986; Arno 1985; Barrett and Arno 1982; Houston 1973; Lewis 1985; Phillips 1985). Was this the case in the Yellowstone region? Certainly there is a need for a team of ecologists, archeologists, and anthropologists to cooperatively synthesize and report on what is known and what can be reliably inferred about the role of native Americans in the Yellowstone region.

To know what the northern Yellowstone was like in pristine times, we also need to understand the role of an intact fauna of large predators other than man. The wolf has been missing from the Yellowstone region since the early 1900's. If ungulates have been present in the Yellowstone region since suitable habitat developed sometime following deglaciation, as I believe they have been, then the large predators that preyed on those ungulates, especially the wolf and mountain lion (Felis concolor), also would have been present. What effects would they have had in pristine times?

Most researchers recognize the difficulty of determining the role of predators in extant predator/prey systems; even with detailed studies (Theberge and Gauthier 1985; Andrewartha and Birch 1984:88-89; Taylor 1984:33; Mech 1984:189-190,196; Gassaway et al. 1983:2,41; Connolly 1978:375,386). Thus we may be presumptuous to try and describe the role of predation in ecosystems that existed hundreds of years ago. Nevertheless, in recent years there has been growing recognition that predation likely influences the size and dynamics of ungulate populations and their distribution more than previously thought (Bergerud 1983a,c,d; Carbyn 1983; Connolly 1978:393-394; Gassaway et al. 1983:41,43; Mech 1984:189-190; Peek 1980:221; Peterson et al. 1984: 1351; U.S. Fish and Wildlife Service 1984:63; Van Ballenberghe 1985:2). In some cases, or at times, predation may be an important factor limiting the numbers of some ungulate species. It has also become apparent that in a multi-species predator/prey system, such as the one that probably characterized the Yellowstone region in pristine times, the phenomenon of predators switching their effects among prey species can influence their population dynamics and the relative numbers of the several prey species (Bergerud 1983a,b, 1984; Burles

and Hoefs 1984; Carbyn 1983; Connolly 1978). There is also greater appreciation than earlier that predators can influence the distribution of a multi-species ungulate fauna (Connolly 1978:389; Edwards 1983;185; Nelson and Mech 1981:43-44), and that this influence might be most pronounced in temperate, mountainous ecosystems such as the northern Yellowstone where snow conditions are a primary ecological force that ungulates must contend with. Finally, where man is an important predator on ungulates, as some have proposed was the case for native Americans in pristine times (Chase 1986:97-105), predation by man and by nonhuman predators can be additive rather than offsetting and can have significant limiting effects on ungulate populations (Connolly 1978, 1981; Gassaway et al. 1983; Hauge and Keith 1981:595; Van Ballenberghe 1985).

Thus it seems likely that an intact predator fauna influenced the size and dynamics of the several ungulate species populations and the interrelationships between them to an unknown degree, but more than previously thought. It seems unlikely, however, that over the long term, predation by nonhumans kept ungulates from being food-limited. But an intact predator fauna may have had a more significant influence on the distribution of ungulates within the northern Yellowstone ecosystem, particularly during winter. Predators may have caused fewer ungulates, particularly elk, to spend less time in areas within the Park with deeper snow and caused more of them to spend more time and at higher density at lower elevation, more snowfree areas in more northerly parts of the ecosystem where they may have been less susceptible to predation.

In summary, I don't believe we have the basis for even speculating about the size and dynamics of ungulate populations in pristine times or the proportions of the total biomass of ungulates that the various species represented then. All things considered, however, it seems more likely than not that, with or without the influence of native Americans, fewer ungulates, particularly elk and bison, spent less time during winter on the higher elevation, eastern portions of the winter range within the Park during pristine times than during modern times. This is important to interpreting the nature of the coevolution of ungulates and vegetation on the winter range, particularly within the Park, and suggests that the vegetation evolved with less influence from ungulates than has occurred in modern or historical times, but that ungulates and the vegetation did coevolve. Just how much less effect ungulates had in pristine times is unknown and will probably remain unknown.

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